

SOCRANSKY 1968). Some work on the effect of protein-deficient diets on the bones of different genera of rat, including the rice rat, was reported by PACK and LUCAS (1971). The rice rats used in this work came from the daughter colony originally established by rats sent from the Dundee colony.

The general characteristics of the rice rat skull are more clearly shown in the drawings than in lengthy descriptions. On examination the skull is found to be fairly large, with flattening occurring over the dorsal region. The superciliary (supraorbital) ridges are definitely everted and projecting resulting in an increase in the breadth of the skull across the orbits posteriorly. In a similar way, the zygomatic complex shows a wide spreading while the anterior palatal foramina are long — reaching back to a line drawn at right angles to the foramina and joining the right and left first maxillary molar teeth. The frontal bones taper into a narrow point posteriorly in the median line between the parietal bones. The interparietal bone is small and its anterior border forms a straight line while a poorly defined median angle occurs posteriorly. The mandible has a broad angle and the coronoid process reaches above the level of the condylar process. It is proposed, at a later date, to publish a more detailed account of the individual bones forming the rice rat skull and of the dentition.

When attempting the description of the morphology of a particular rodent skull about which there is only a limited amount of known data, it is natural to try and attain perspective by using some baseline whereby comparisons can be demonstrated. To allow such comparison to be made, the well-documented albino laboratory rat (*Rattus norvegicus*) proved to be an excellent foil in previous work (PARK 1972) and has been used in the present work. When the skulls of these two species are compared several differences are revealed besides the more obvious one of size. The following list can only be regarded as a tentative one and used as a rough guide until further information on the variations are established.

1. The antero-posterior alignment of the maxillary and mandibular tooth rows is almost parallel in the rice rat whereas in the albino laboratory rat, greater curvature and a slight divergence posteriorly is shown.
2. The angulation of the mandibular molar teeth towards the median sagittal plane is more pronounced in the albino laboratory rat.
3. The anterior palatine foramina of the rice rat are much longer than those of the albino laboratory rat.
4. From both dorsal and ventral aspects, the squamosal bones of the rice rat as they curve laterally and anteriorly to meet the zygomatics, have small but definite notches medial to the zygomatic process.
5. The frontal bones of the rice rat taper into a narrow point posteriorly, in the median line between the parietal bones — along the coronal suture line. This particular suture junction is relatively straight in the albino laboratory rat.
6. The interparietal bone is very narrow in the rice rat, compared with the albino laboratory rat, and forms a relatively straight line along its anterior border. In the albino laboratory rat, the anterior border ends in a small notch or wedge.
7. In the mandible, the coronoid process is more vertically orientated in the rice rat and also more pointed. As a result of this the mandibular notch is deeper and wider than in the albino laboratory rat.
8. The angular process of the mandible of the rice rat is shorter and rounder, and does not extend so far posteriorly beyond the condylar process as it does in the albino laboratory rat.

### Summary

General morphological characteristics of the skull of the recently introduced rice rat have been described following some 15 generations under laboratory conditions. Approximately

100 rats aged from 1—16 months were examined and a series of drawings made representing the more prominent skull characteristics, based on the male sample. For purposes of perspective, the skull of the albino laboratory rat (*Rattus norvegicus*) was used.

### Zusammenfassung

#### *Biologie der Reissratte (Oryzomys palustris natator) im Labor*

#### *II. Allgemeine Schädelmorphologie*

Es wurden allgemeine Schädelmerkmale von Reissratten beschrieben, die sich seit 15 Generationen unter Laborbedingungen befinden. Ungefähr 100 Ratten im Alter von 1—16 Monaten wurden untersucht; durch eine Serie von Zeichnungen wurden für die Männchen die auffallenden Schädelmerkmale herausgearbeitet. Als Grundlage der Beschreibung wurde der Schädel der Laborratte benutzt.

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## On functional fusions in footbones of Ungulates

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### Introduction

During evolution, especially in the Orders Artiodactyla and Perissodactyla we find a reduction of number of footbones, elongation of the metapodials and phalanges and sometime fusions of bones.

Those changes can be explained functionally: to provide the animal with a locomotion which is more efficient in running. Usually the tibia and fibula, radius and ulna fuse tightly together, which restricts the lateral movement and the motion is confined to the sagittal plane. In the ruminantia we find also the metapodials of the third and the fourth digit joined into one cannon bone. Some of the carpals and tarsals fuse also like navicular and cuboid, trapezoid and magnum, giving the carpal and tarsal joints more strength to lateral movements.

The fusions cannot be followed step by step due to fact that the fossil record is not complete. Probably the changes, or in other words the selection of the genetically fixed favourable fusions, take place in a rather short period.

The purpose of this paper is to describe some less common fusions in Perissodactyla and Artiodactyla and further to attempt to give a functional analysis, and the evolutionary meaning of those fusions.

## Material studied

*Parahippus blackbergi* stored in University of Florida, and the Museum of Comparative Zoology, Harvard.

*Phanourios minor* and *Cervus cretensis* stored in the Geological Institute, Utrecht.

*Myotragus balearicus* stored in the British Museum of Natural History and Deya Archaeological Museum.

Cervids from Gargano, stored in the Rijksmuseum voor Geologie, Leiden. Recent comparative material from several museums.

## Magnum with trapezoid in equids

In three of the fifteen available magnums of *Parahippus blackbergi* from the miocene of Thomas farm (Florida), the trapezoid is completely fused with the magnum (plate I, fig. A), while in the others the bone structure where the two bones are in contact, suggests that there was no movement between the bones. This was learned from the posterior part of the trapezoid and magnum. On the magnum we find at the medial posterior side a tuberosity which must have been in contact with a similar tuberosity on the trapezoid. This contact was not a facet as found in *Equus* (SONDAAR 1968) but a rough area.

If we try to analyse the functional meaning of this fusion in *Parahippus*, it is necessary to consider the bones separately. The scaphoid transfers the weight from the body to the magnum and trapezoid and those bones shift the weight to the third and second metacarpal respectively.

During the evolution of the horse we see a relative reduction of the second digit after a major change between the Anditheriinae and Hipporioninae (SONDAAR 1969).

The genus *Parahippus* was the first representative in the family of the Equidae in which this change occurred, namely the lateral flexibility of the foot became restricted; further a clear lengthening of the central phalanges lifted the foot from the ground and led to loss of its pad.

The function of the lateral metapodials became reduced. When we follow the changes from *Parahippus* towards *Equus* we see, by changes in shape, size and position of the articulation facets of carpal bones, that more and more weight will be shifted towards the central metacarpal.

This is evident when we follow the changes in the trapezoid. In *Equus* for example this bone has a clear facet, on the posterior side, articulating with the third metacarpal so more of the weight is borne by this metacarpal.

The contact between the trapezoid and magnum is always by clear articulation facets. The described fusion in *Parahippus blackbergi* is clearly an exception in the phylogeny of the horse. This fusion can be explained in two different ways; pathological or functional. Though the fusion is complete, in only three of the fifteen magnums. We can exclude the pathological explanation as all other specimens show that there was no movement between magnum and trapezoid and the whole population cannot have been pathological. A good functional explanation exists: by fusion of the trapezoid and magnum more of the weight is borne by the third metacarpal at an evolutionary stage in which the function of the second metacarpal was reduced. We may mention a relevant parallelism with the Ruminantia in which the trapezoid and magnum are also fused (YALDEN 1971) but here this fusion is total. Concluding we may say that the fusion of trapezoid and magnum had a functional meaning to transfer more weight to the central metacarpal and in this *Parahippus blackbergi* was more advanced than the recent *Equus*. The question why this configuration which proved to be so successful in Ruminantia failed in the Equidae must stay open. Of course



we can speculate that the *Parahippus* of Florida was local evolved and isolated branch of the equids which failed to invade central North America by a less adapted chewing mechanism.

### Navico — cuboid with the cuneiformes and the metatarsals in ruminants

Common characters of the fossil ruminants from the mediterranean islands are a secondary shortening of the lower part of the leg, a short skull, hypsodont teeth and further fusion of the tarsal bones. We observed these characters in:

- a. *Myotragus balearicus*, a bowid from the pleistocene of Mallorca.
- b. *Cervus cretensis*, a deer from the pleistocene of Crete.
- c. *Cervus elaphus* var. *barbarus*, a deer from the pleistocene of Malta.
- d. A still undescribed deer from the miocene of the Gargano region in Italy (FREUDENTHAL 1971).

It is remarkable that these skeletal characteristics occur in different families of the artiodactyla, on different islands and in deposits with a different geological age.

Normally in ruminants the following tarsal bones are fused:

- a. Metatarsus III and IV (cannon bone)
- b. Navicular and cuboid (navico-cuboid)
- c. Cuneiforms II and III (great cuneiform)

The further fusions of the tarsal bones from the ruminants of the endemic islands faunas are:

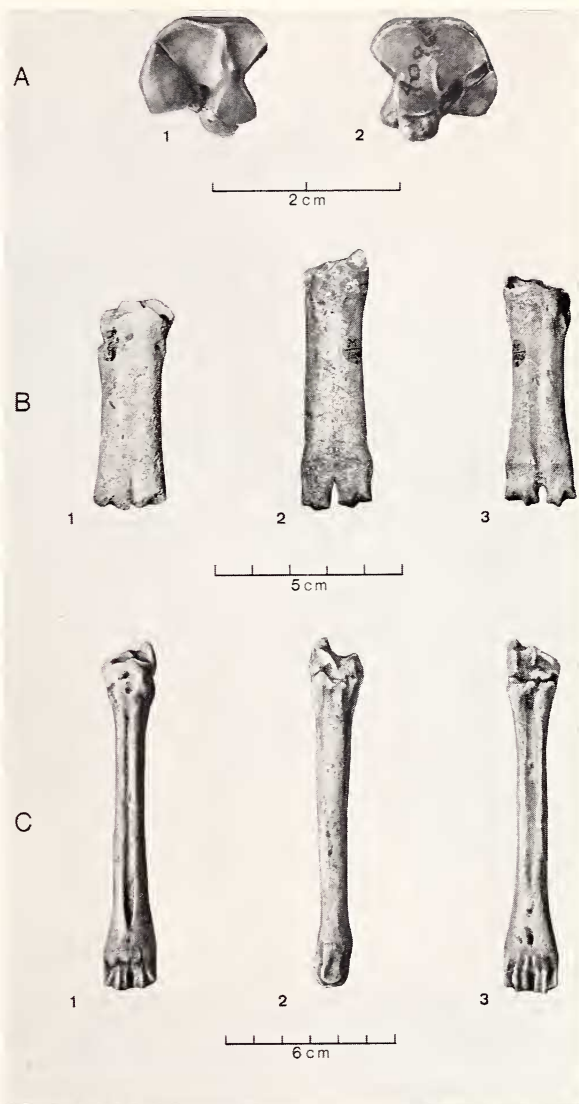


Plate I. A = *Parahippus blackbergi*, University of Florida, coll. no. 4096, magnum fused with trapezoid sin. 1 = proximal view; 2 = distal view. — B = *Myotragus balearicus*, British Museum coll. no. 1106, navico-cuboid-cuneiforme complex fused with the cannon bone dorsal views. 1 = juvenile individual; 2 = young individual; 3 = adult individual. — C = *Cervus cretensis*, coll. Geol. Inst. Utrecht, navico-cuboid-cuneiforme complex fused with the cannon bone dext. 1 = dorsal view; 2 = lateral view; 3 = volar view.

- d. Cuneiforms with the navico-cuboid (plate II, fig. 3)
- e. Frequently this navico-cuboid-cuneiforme complex is fused with the cannon bone (plate I, fig. B and C)<sup>1</sup>

In order to understand the functional significance of these further fusions it is necessary to investigate the function of these tarsal bones in recent ruminants.

Plate II, fig. 2A shows that two tendons are attached to the cuneiform I (small cuneiform): in the recent *Antilope cervicapra*.

On the lateral side a strong tendon leading to the musculus peroneus longus and on the medial side a smaller tendon leading to musculus tibialis. The tendon of musculus peroneus longus passes, in the direction of the lateral side of the navico-cuboid, through a groove which divides the facet on the navico-cuboid for the cannon bone in two parts (plate II, fig. 2A, facets d and e) and continues on the lateral side of the navico-cuboid.

Handling fresh dead material it appears that contraction of the musculus peroneus longus results in a slight rotation of the cannon bone caused by the movement of the cuneiform I, in such a way that the plantar face of the foot turns to the lateral side and as a second function the muscle contributes to the extension of the tarsal joint.

This rotation of the cannon bone seems to be related to the ability of ruminants to zigzag at full speed in order to escape predators. The contrasting construction of the tarsal joint of the giraffe, in connection with its inability to zigzag, seems to confirm this explanation. In the giraffe the cuneiform I is fused with the cuneiform II/III (plate II, fig. I A and I B) and the groove for the tendon of musculus peroneus longus on the navico-cuboid has disappeared and the facets for the cannon bone become united (plate II, fig. I B facets d and e).

A typical aspect of island faunas is the absence of predators and as a consequence of this, speed and zigzag mechanism have loste their functional significance for the ruminants living on those islands.

As a result of the fusion of tarsal bones the tarsal joint becomes more solid. This, with the shortening of the metatarsals and the phalanges, gives a foot construction which is advantageous for a low speed locomotion in a varied environment and what could be called a low gear locomotion.

### Navicular with one or more cuneiforms in hippos

From 25 naviculars of *Phanourias minor*, seven are fused with the cuneiform III, one with cuneiform II and III, one with cuneiform I, two with all cuneiforms (I, II and III).

*Phanourias minor* is endemic to the pleistocene of Cyprus and most probably descended from *Hippopotamus amphibius*. In the fossil and recent Hippopotamidae such fusions are otherwise unknown. BOEKSCHOTEN and SONDAAR (1972) note in *Phanourias minor* that the movement in lateral sense of the legs are restricted, but more extended in anterior-posterior sense than in *Hippopotamus amphibius*. This is learned from the tarsal joint where the movement between cuboid and navicular is more restricted while more movement between these two bones and the astragalus is possible in anterior-posterior direction. In this the hippo from Cyprus resembles *Hippopotamus creutzburgi* from Crete. This change in movement of the joints can be explained by an adaption to an island life where natural meadows along big rivers were absent and so a locomotionary system adapted to walking, to reach the more rugged grazing sides was a necessity, BOEKSCHOTEN and SONDAAR (1966).

<sup>1</sup> The first author has the intention to give quantitative datas in a further publication.

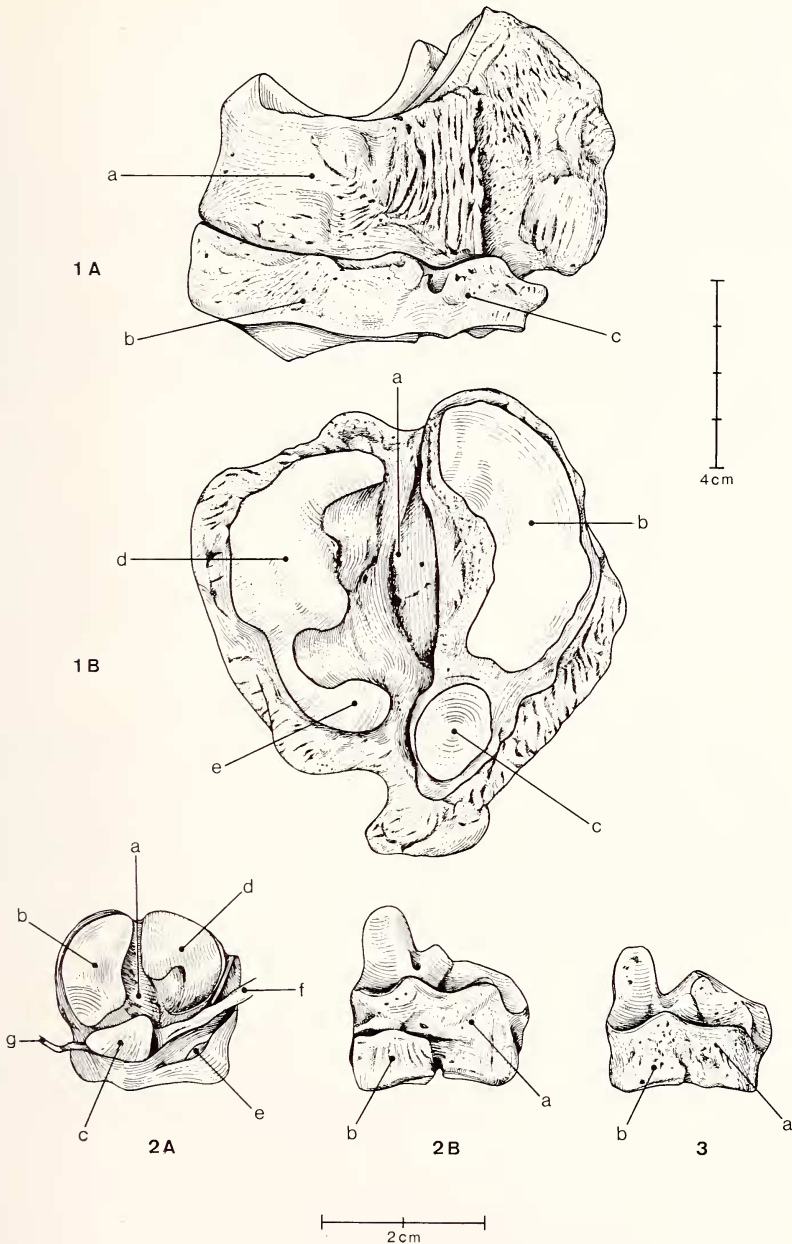


Plate II. — Fig. 1. *Giraffa camelopardalis* dext. Coll. Zool. Museum, Amsterdam (No. 964). A = medial view; B = distal view. — Fig. 2. *Antelope cervicapra* sin. Coll. Geol. Inst. Utrecht. A = distal view; B = dorsal view. — Fig. 3. *Cervus cretensis* sin. Coll. Geol. Inst. Utrecht, dorsal view. a = navico-cuboid; b = cuneiforme II/II; c = cuneiforme I; d = anterior facet for the cannon bone; e = posterior facet for the cannon bone; f = tendon leading to musculus peroneus longus; g = tendon leading to musculus tibialis.